

The Valid Varieties of *Pellaea andromedaefolia*THOMAS R. PRAY¹

Since *Pellaea andromedaefolia* (Kaulf.) Fée was first described in 1824, various forms of this Californian species have received systematic recognition. In a monographic revision of section *Pellaea*, to which the species belongs, Tryon (1957, p. 179) regarded none of these variants as taxonomically significant. Certainly anyone familiar with this species in the field, where it grows under a variety of conditions, will recognize the plasticity of the species in response to its environment. Variety *rubens* D.C. Eaton and var. *gracilis* Summers ex Farlow undoubtedly are examples of simple, environmentally induced variants. Regarding the possible significance of other variant forms of *P. andromedaefolia*, some observations concerning a dwarfed specimen are in order. This specimen (*Whitehead 5050*) is quite fertile and is apparently a mature individual. Its leaves are fully tripinnate and it agrees with var. *andromedaefolia* in other respects. The leaves are only 16 cm high however, and the segments are very small, averaging only 4 mm long, compared to the usual 7–10 mm. In spite of its size, young sporophytes raised from its sexual gametophytes were all typical of var. *andromedaefolia* and showed no trace of the diminutive features of the parent plant. Thus, unusually small size, in this case at least, was environmentally induced and not genetically fixed.

On the other hand, var. *pubescens* D.C. Eaton is decidedly distinct. The distinction between this variety and typical *P. andromedaefolia* is the subject of this paper.

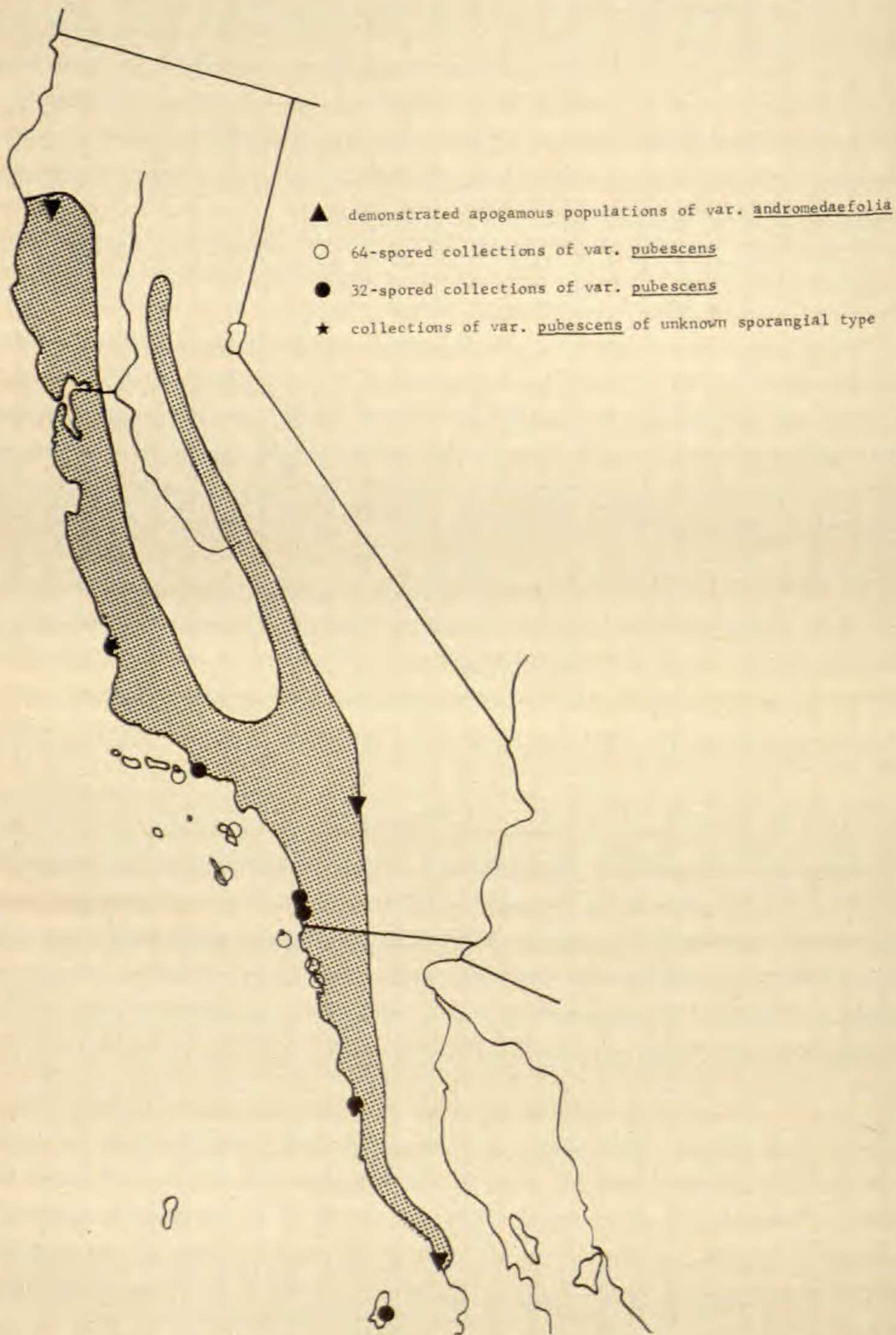
Most local floras have ignored the pubescent form of *P. andromedaefolia*. The most recent, that of Munz (1959), mentioned it as occurring in the vicinity of San Diego. Tryon (1957, p. 182) recognized that the pubescent form was from the southern portion of the species' range and stated that it was distinguished by having 32-spored sporangia. The typical glabrous form was said to be

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64-spored. The implication was, therefore, that var. *pubescens* was an apogamous form of a sexual species, although at that time there was no direct evidence of apogamy. As the result of extensive field studies, transplant experiments, and the raising of numerous plants from spores, I have found that these statements represent a great oversimplification of the situation.

Plate 7 illustrates the distribution of the species (see *Table I* for a full list of the collections cited in this study). Variety *andromedaefolia*, with glabrous stipes and rachises and glaucous leaf segments, ranges from northern California—a report from southern Oregon is doubtful, as stated by Tryon (1957, p. 182)—southward through the state and along the west coast of Baja California Norte, Mexico, to the region of Bahia de Sebastian Vizcaino. In central California it extends inland to the foothills of the Sierra Nevada and in southern California it occurs along the western borders of the Colorado Desert. In the southern part of its range it occurs on some of the offshore islands. While var. *andromedaefolia* was well distributed at one time on Santa Catalina Island, only a single collection has been made in recent years (*McNeil 76*). Much searching in appropriate habitats has revealed that it is now extinct there, or nearly so. Similarly, three days of searching on Santa Cruz Island produced a single specimen of the typical variety on an inaccessible cliff where it could not be collected.

Variety *pubescens*, with puberulent stipes and rachises and non-glaucous segments, occurs from San Luis Obispo south to Cedros Island. It appears to be a strictly coastal ecotype, a fact which has not been recognized previously. All the material I have seen is from coastal bluffs and hills and at or near the mouths of coastal canyons. The type of var. *pubescens* came from the San Luis Obispo area (Eaton, 1878). Its occurrence there has been recently confirmed (Hoover, 1966). I have not seen any material from this most northern locality, but Hoover's comments suggest that his material is the same as that which I have studied. The most northern collections available to me came from southern Ventura County (Point Mugu). I know of no locality between this and San Luis Obispo, although suitable habitats in



MAP OF THE DISTRIBUTION OF *P. ANDROMEDAEOFOLIA*. SHADED AREA INDICATES THE GENERAL DISTRIBUTION OF VAR. *PUBESCENS* AND VAR. *ANDROMEDAEOFOLIA* IN CALIFORNIA AND MEXICO.

the intervening regions have been searched carefully. Although the coastal area between Point Mugu and Los Angeles seems a likely habitat, I know of no collections of var. *pubescens* from there. It does occur to the south in San Diego County, where I have made several collections. On the offshore islands the presence of var. *pubescens* is definitely established for Anacapa, San Clemente, South Coronado and Cedros Islands. It may also have occurred on Santa Catalina, but several personal attempts to find extant material of this variety were unsuccessful. The floras of these islands have been decimated by overgrazing of sheep, or goats, or both to such an extent that it is no longer possible to find many species where they were once collected. For Mexico, I have seen material from Ensenada south to San Quintín.

From the relatively small amount of material studied it would appear that the two varieties do not usually occur in the same locality. The typical form is rarely found in the exposed maritime environment to which var. *pubescens* is largely restricted. The only instance of sympatry observed was at Point Mugu, where there were a few, very small individuals (2028) of the typical variety in a population predominantly of the pubescent variety.

D. C. Eaton (1878) distinguished var. *pubescens* only by the presence of the fine pubescence on the stipes and rachises and cited a specimen from San Luis Obispo (*Mrs. R. W. Summers*). Apparently neither he nor anyone since has noticed that, although the pubescence provides one obviously distinguishing feature (clearly visible only when magnified), several others are equally obvious. In life the pinnules of var. *pubescens* are succulent and are bright green and shiny on the upper surfaces. Upon drying the upper surface looks resinous. The segments appear to be thicker than those of the typical variety; sections of the pinnules did not confirm this, however. On the other hand, the pinnules of var. *andromedaefolia* are consistently at least slightly glaucous and dull. The development of anthocyanins in the leaves as a response to drought or extreme exposure is common to both forms. The vein pattern is clearly evident on the upper surfaces of the pinnules in fresh condition in var. *pubescens*, whereas this feature is obscure

TABLE I. LIST OF COLLECTIONS¹

<i>Coll. number</i>	<i>Locality</i>	<i>Sporangial type</i>
VARIETY ANDROMEDAEFOLIA		
1668	Santo Tomas, highway #1 at Km 193, Baja Calif. Norte, Mex.	64-spored
1669	San Juan Canyon, Orange Co., Cal.	64-spored
1909	Andreas Canyon, Palm Springs, Riverside Co., Cal.	32-spored
2028	Point Mugu, Ventura Co., Cal.	64-spored
Dunkle 1881	Santa Catalina Isl.	64-spored
Dunkle 2865a	Santa Catalina Isl.	64-spored
Garth 1089	Andreas Canyon, Palm Springs, Riverside Co., Cal.	32-spored
McNeil 76	Holland's Cove, Santa Catalina Isl.	Immature
J. H. Thomas 8223 (DS)	Miller's Landing, Baja Cal. Norte, Mex.	32-spored
Tryon & Tryon 5556 (GH)	Redway, Humboldt Co., Cal.	32-spored
Wiggins 9967 (DS)	40 mi. NE of El Rosario, Baja Cal. Norte, Mex.	64-spored
Whitehead 5050	no data	64-spored
VARIETY PUBESCENS		
1665, 1666	Ensenada, S on highway #1 at Km 66, Baja Cal. Norte, Mex.	64-spored
1667	as above at Km 81	64-spored
1906, 1907, 2027	Point Mugu, Ventura Co., Cal.	32-spored
2056, 2057	Del Mar, San Diego Co., Cal.	32-spored
3215	grown from spores of 1665	—
Cooper 2172	Ensenada, Baja Cal. Norte, Mex.	—
Dunkle 2043	Little Gibraltar, Santa Catalina Isl.	64-spored
Dunkle 4262	Johnson's Trough, Baja Calif. Norte, Mex.	—
Dunkle 7663	Anacapa Isl.	64-spored
Elmore 383, 413	San Clemente Isl.	64-spored
Epling & Stewart (DS)	San Quintín, Baja Cal. Norte, Mex.	32-spored
Ferris 8511 (DS)	San Vicente, Baja Cal. Norte, Mex.	Immature
Moran 8301	South Coronado Isl., Mex.	64-spored
Moran 1065 (DS)	Cedros Island, Mex.	Immature

<i>Coll. number</i>	<i>Locality</i>	<i>Sporangial type</i>
UCBG 62.432-1	Cultivated. Original from San Diego Co., Cal. (<i>Hutchison 2160</i>)	32-spored
<i>Wiggins 11974</i> (DS)	South Coronado Isl., Mex.	Immature

¹ All collections of var. *pubescens* seen are included. Only those of var. *andromedaefolia* especially pertinent are cited; many others have been examined. Collection numbers not otherwise identified are those of the author. Specimens are deposited in the herbarium of the Allan Hancock Foundation (AHFH), University of Southern California, unless indicated otherwise.

in the typical variety. Unfortunately, this characteristic sometimes becomes less evident in drying. The degree of lamina dissection is most useful in mature plants. The leaves of the typical variety are usually tripinnate (rarely quadripinnate), even in rather depauperate specimens. Variety *pubescens*, in contrast, has bipinnate leaves, even in the largest plants. The largest leaves may have a very few ternate pinnules in the basal pinnae. In the typical variety many of the pinnules commonly have 5-7 (occasionally up to 10) segments; pinnules even in the upper portion of the leaf are usually at least ternate. Correlated with the simpler leaves of var. *pubescens* is the increased size of the ultimate segments. This distinction is well demonstrated when the two varieties are cultivated under similar circumstances, but segment size varies with environmental conditions, so herbarium material can not be reliably distinguished on this basis. The stature of the two varieties also distinguishes them. Under the best conditions the typical form may produce leaves as much as 80 cm long. The largest specimens of var. *pubescens* studied had leaves only 35 cm long, and most specimens were much smaller. No cultivated material has been observed to exceed this height. The stouter and more rigid stipes and rachises are correlated with the shorter stature.

Among the distinctive features of var. *pubescens*, the non-glaucous segments and bipinnate leaves can be used to identify it, even if it is not pubescent. One collection from Santa Catalina Island (*Dunkle 2043*) has all of the characteristics of var. *pubescens* except pubescence. The collection consists of several old leaves

only, and it is possible that this latter feature has been lost with age. An effort was made to recollect this fern from the Dunkle locality, but no plants of either variety were found. This specimen is the only evidence I found for var. *pubescens* on Santa Catalina. A collection from Anacapa Island (*Dunkle 7663*) also lacks the puberulence typical of var. *pubescens*, but is otherwise indistinguishable from material of this variety. Tentatively, therefore, it is listed as var. *pubescens*. Perhaps these two collections are hybrids of the two varieties. It should be noted that the insular collections of var. *andromedaefolia* do tend to be smaller plants with less complex leaves than is typical for the variety. Whether these represent local variants cannot be decided on the basis of the meager material available.

Under cultivation the differences between these two varieties were maintained and were especially obvious when the plants were compared side by side. Both varieties were also grown to maturity from spores, and the progeny retained the distinguishing features of the parents. No intermediates have been discovered in the field. At Point Mugu, the only locality where the two varieties were observed growing together, the plants of var. *pubescens* were apogamous, whereas the plants of var. *andromedaefolia* were 64-spored and presumably had sexual gametophytes. Therefore, the lack of intermediates between the varieties is understandable.

Tryon (1957) reported that the pubescent form is 32-spored, but further study has shown that no such correlation between spore number and morphology exists. The material from Point Mugu (1906, 1907) is 32-spored and reproduces by apogamy (Pray, ms.). Material from San Diego County also is 32-spored and apogamous (2056, 2057, *UCBG 62.432-1*.) In contrast, the plants on the islands that are directly offshore from these localities apparently are sexual. Among the insular collections cited, some were too immature to determine their spore number and probable reproductive method. Only *Elmore 383* and *413* from San Clemente and *Dunkle 7663* from Anacapa had spores; these are all 64-spored. Collections from northern Baja California (1665, 1666, 1667) and

adjacent South Coronado Island (*Moran 8301*) are 64-spored and produce sexual gametophytes. The southernmost collection, from San Quintín (*Epling & Stewart*), is probably 32-spored, although a positive count could not be made. Tryon (1957) reported a Cedros Island collection to be 32-spored. The distribution pattern for apogamy in var. *pubescens* based on available material is puzzling (*Plate 7*). If the present pattern can be taken as a reflection of the history of this variety, then perhaps var. *pubescens* had its origin in northern Baja California from whence it spread to the Coronado and Channel Islands. On the mainland it may have moved both north and south through the formation of apogamous races which apparently reached the islands only in the south.

Although most collections of var. *andromedaefolia* are 64-spored (and those investigated produced sexual gametophytes), 32-spored and apogamous individuals are scattered throughout the range of this variety: Humboldt County (*Tryon & Tryon 5556*), Sierra Nevada foothills near Yosemite, (Tryon, pers. comm.), Palm Springs (1909, *Garth 1089*), and Baja California (*Thomas 8223*, which is the most southerly record for the typical variety). All other determinable Mexican collections are 64-spored. All the insular material for which a spore count is available is 64-spored. Thus, in the typical variety apogamy is sporadic; it seems likely that each of the apogamous populations has had a separate origin. Differences among the gametophytes from each of those that has been investigated support this assumption (Pray, 1968).

There does not appear to be any correlation between morphology and spore number in either variety. The only method by which apogamous populations can be identified is by spore count. This contrasts with the closely related *P. ovata*, which also has both 64- and 32-spored forms. All of the material of *P. ovata* studied thus far has shown that the 64-spored plants are glabrous and produce sexual gametophytes, whereas the 32-spored plants all show varying degrees of pubescence. All of the latter type that have been tested have produced apogamous gametophytes.

It is clear that the differences between var. *andromedaefolia* and var. *pubescens*, which are summarized in *Table II*, are suffi-

ciently marked to merit the systematic recognition of var. *pubescens*. In my opinion, the two varieties are comparable to good subspecies in other groups. To a very remarkable degree the situation in *P. andromedaefolia* parallels a similar situation in another Californian species, *P. mucronata* (D. C. Eaton) D. C. Eaton. The general distribution pattern of the two species is very similar (Tryon, 1957), and in fact they are often in the same

TABLE II. COMPARISON OF THE TWO VARIETIES OF *P. ANDROMEDAEOFOLIA*

Character	Variety <i>andromedaefolia</i>	Variety <i>pubescens</i>
Range	cismontane & insular Calif.; western Baja Calif. Norte, Mex.	coastal & insular So. Calif.; adjacent Mex. to Cedros Island
Sporangial type	64-spored; sporadic 32-spored populations	64-spored Channel Isls. and northern Baja Calif. Norte; 32-spored, southern Baja Calif. Norte, Mex., Cedros Isl. and southern Calif.
Height	up to 80 cm	less than 35 cm
Leaf form	tripinnate, many pinnules with 5-7 segments	bipinnate, a few ternate pinnules; ultimate segments usually larger
Stipe & rachis	glabrous, slender	puberulent, stouter
Leaf color	dull, glaucous	shiny, bright green
Venation	evident on lower surfaces only	prominent also on upper surfaces, especially in living state

localities; in these *P. mucronata* will be found in drier, more exposed habitats. *Pellaea mucronata* is represented throughout most of its range by the common form, var. *mucronata*, characterized by finely divided, tripinnate (rarely quadripinnate) leaves. In the higher mountains of central and southern California the typical variety is replaced by a montane ecotype, var. *californica* (Lemmon) Munz & Johnston, which differs in its smaller stature and in its bipinnate and more compact leaves. Thus, both of these fairly widespread species appear to have evolved specialized and reduced ecotypes to fit more extreme environments, in one case the maritime environment, in the other the montane.

The parallel may be extended even further, for each of these species also has a counterpart species in the southwestern region of the interior of the continent. Here *Pellaea longimucronata* replaces *P. mucronata*. Their relationship is sufficiently close to permit hybridization at points of contact (Pray, 1967). In the same region *P. intermedia* replaces *P. andromedaefolia*. In this case there is a considerable gap between the ranges of the two species. In spite of the remarkable similarity between *P. intermedia* and *P. andromedaefolia* var. *pubescens* it seems unlikely that there is a direct relationship because of the specialized ecology of the latter. More probably, these two are parallel developments and, if closely related, it is through var. *andromedaefolia*. Nevertheless, if the geographic origin of herbarium specimens of var. *pubescens* were not known, these would be easily confused with *P. intermedia*, which is also characterized by bipinnate leaves with puberulent stipes and rachises. Probably the simplest method by which they may be distinguished, as indicated in Tryon's key (1957), is the very clear vein pattern evident on the underside of the segments of *P. andromedaefolia* in contrast to the unveined appearance of *P. intermedia*. When compared closely, the rhizome scales are also distinctive, although they are of the same general type. Those of *P. andromedaefolia* var. *pubescens* are about twice as broad at the base and appear lighter when the rhizome is viewed with a hand lens. The dark central band extends about $\frac{1}{2}$ to $\frac{2}{3}$ the length of the scale, whereas in *P. intermedia* the central band extends to the scale tip. The clear margins of the scale seem a bit broader in var. *pubescens*, but the difference in this respect is not obvious.

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Petiolar Shoots in the Dennstaedtioid and Related Ferns¹

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Stelar branching patterns and bud formation in the Filicales have been investigated little since the beginning of this century. Fern stems may branch by dichotomy, axillary buds, or buds not clearly in the axils of leaves. Buds from frond bases were reported and described by Gwynne-Vaughan (1903) for a number of ferns. In a monographic work on *Dennstaedtia punctilobula* (Michx.) Moore, Conard (1908) described in detail the anatomy of shoots from the petiole bases of this fern. Webster (1958) observed dormant buds on the leaf bases in *Pteridium aquilinum* var. *latiusculum*, but none were seen to elongate. Further references to budding of ferns are scattered, and the phenomenon is mentioned only briefly, as in Wardlaw (1952) and Wagner (1963), for *Matteuccia*, *Onoclea* and *Dryopteris*. None of these workers has attributed any phylogenetic or taxonomic importance to the phenomenon, and, in view of the meager information available, it is appropriate that more comprehensive studies be undertaken.

In the summer of 1967 we participated in a course in the biology of tropical pteridophytes offered by the Organization for

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